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Holling's functional response model as a tool to link the food-finding mechanism of a probing shorebird with its spatial distribution

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Summary

1. Knots *Calidris canutus* are high-arctic breeding shorebirds which spend the non-breeding season in intertidal areas where they feed on small buried molluscs which are swallowed whole. We tested whether their intake rate can be adequately described by a functional response model (the disc equation of Holling) assuming prey detection by direct touch.

2. Knots were fed two bivalve species (*Macoma balthica* and *Cerastoderma edule*) of different size and at different density and in *Macoma* at variable depth on small areas of soft sediment. Five different individuals were used in feeding trials during which six prey were allowed detection and ingestion.

3. Knots perfectly obeyed the two basic assumptions of Holling's disc equation: neither the instantaneous area of discovery nor the handling time changed with variation in prey density.

4. However, two predictions for prey perception by direct touch (that the instantaneous area of discovery is a positive function of shell size and a negative one of prey depth) were rejected. The instantaneous area of discovery was usually also higher than predicted from the area touched by probing knots.

5. Knots may, therefore, use a 'remote sense' to locate buried hard-shelled prey. Gerritsen, van Heezik & Swennen (1983) showed that knots do not use taste to discover bivalves at a distance. We argue that the detection involves a self-induced pressure mechanism rather than a passive sense for vibrations, since it is unlikely that static bivalve prey emit such signals just after experimental handling.

6. Whatever the exact prey detection mechanism, the recorded (high) value for the instantaneous area of discovery of deep-living bivalve prey is in accord with the observation that knots use large areas of intertidal flat in the western Dutch Wadden Sea where bivalve stocks are too low to support knots according to a previous functional response model invoking direct touch.

Key-words: foraging, habitat use, intertidal ecosystem, knots *Calidris canutus*, prey detection.

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Introduction

Understanding habitat use and spatial dynamics of a predator species not only requires knowledge about strategies of prey selection and the assessment of feeding habitats (e.g. Stephens & Krebs 1986), about ways in which potential prey can avoid being detected or

being captured (e.g. Endler 1991) and about the interactions between competing individual predators (e.g. Milinski & Parker 1991), but also about the precise mechanisms by which predators detect their prey (e.g. Getty & Pulliam 1993). Probe-feeding sandpipers and similar kinds of shorebirds may employ two mechanisms to detect prey buried invisibly in soft intertidal sediments: remote sensing and direct touch. Gerritsen & Meijboom (1986) presented evidence that san-

derlings (*Calidris alba* [Pallas, 1764]) may detect sub-surface polychaetes at a minimal distance of 2 cm, perceiving vibrations made by the moving worms with sensitive mechanoreceptors in their bill tips. Studies of intake rate of free-living oystercatchers (*Haematopus ostralegus* Linné, 1758) (Hulscher 1982; Wanink & Zwarts 1985) and knots (*Calidris canutus* [Linné, 1758]) (Zwarts & Blomert 1992; Zwarts, Blomert & Wanink 1992) searching for buried molluscs have assumed that these birds find their prey by direct touch. Wanink & Zwarts (1985) and Zwarts *et al.* (1992) incorporated touch as the basic mechanism of prey detection in the functional response model of Holling (1959a, b). The present study investigates the assumptions underlying the disc equation (type-2 functional response) and provides an explicit test of the validity of prey detection by direct touch.

Our subjects, knots, usually occur in exposed intertidal habitats, feeding on small bivalves and gastropods that are obtained in a rather stereotyped way, by probing in soft sediments (Prater 1972; Alerstam, Gudmundsson & Johannesson 1992; Zwarts & Blomert 1992; Piersma *et al.* 1993b). The distribution pattern of knots during the nonbreeding season is intriguing, with different segments of the circumpolar breeding population wintering at widely different latitudes along the coasts of all continents (Piersma & Davidson 1992). In addition, the critical availability variables of buried bivalve prey are relatively easy to quantify (Zwarts & Wanink 1982, 1993; Piersma 1987; Zwarts *et al.* 1992; Piersma, de Goeij & Tulp 1993a; Zwarts & Wanink 1993; Tulp & de Goeij 1994). This set of characteristics holds the promise that an elucidation of the basic prey detection mechanism has wide applicability for analyses of the resource base of this category of seasonal migrants.

Experiments were carried out under controlled laboratory conditions. These are much more uniform than those encountered on intertidal flats, but they offer the possibility to vary factors possibly affecting intake rate, such as the density, the size and the depth of buried bivalves independently. Our results hint at undescribed sensory mechanisms (Dusenbery 1992), warranting further study.

THE FUNCTIONAL RESPONSE EQUATION

Based on Holling (1959b), the expected intake rate, dN/dt , must be written as:

$$\frac{dN}{dt} = \frac{aD}{1 + at_h D} \quad \text{eqn 1}$$

where N is the number of prey ingested, t is time (s), a is the instantaneous area of discovery ($\text{cm}^2 \text{s}^{-1}$), D is the prey density (cm^{-2}) and t_h is the (constant) handling time (s). The instantaneous area of discovery, a , is a 'clearance rate', and is also called searching efficiency (Hassell 1982). If there is no

depletion of available prey during the course of the experiment, or if the predator searches completely systematically (Royama 1971; Rogers 1972), Holling's disc equation applies:

$$N = \frac{aDT}{1 + at_h D} \quad \text{eqn 2}$$

where T is the time (s) that the experiment lasts. The product aD usually is called the encounter rate (s^{-1}), and its reciprocal is the search time t_s (s). Hence equation 2 can be rewritten as:

$$N = \frac{T}{t_s + t_h} \quad \text{eqn 3}$$

The second component of the disc equation is the time needed for a predator to handle encountered prey during ingestion (the handling time, t_h). For knots this includes (i) an unmeasurable but probably very short recognition time, (ii) the time for lifting the prey out of the sediment, (iii) the time for positioning the prey in the bill, (iv) the time for swallowing the prey, and (v) the time it takes the bird to move its bill down to go on probing for the next prey (see Gerritsen 1988a: p. 119).

Materials and methods

EXPERIMENTAL DESIGN

In each experimental session individual knots were offered one of two bivalve species: the baltic tellin (*Macoma balthica* [Linné, 1758]) or the edible cockle (*Cerastoderma edule* [Linné, 1767]). The other experimental factors were shell length, prey depth (only for *Macoma*) and prey density. Unfortunately the experimental design was not as balanced as envisioned, among other things due to problems of availability of prey types and experimental animals. The experimental design is given in Table 1.

BIRDS

From September to December 1992, foraging experiments were carried out with five knots. Table 2 summarizes the individual characteristics of the experimental birds. Four birds belonged to the subspecies *islandica* (see Piersma & Davidson 1992 for an overview of knot subspecies and their distribution). They were captured in the Wadden Sea in 1991, and had been kept in captivity ever since. The knots had been fed on trout food-pellets. The only probable bird of the subspecies *canutus*, was an adult bird captured on Texel in the western Wadden Sea in the summer of 1992.

The birds were kept together in small holding cages measuring 240 cm by 60 cm and with a height of 25 cm. The individual experiments were carried out in the same cages by separating one bird from the rest

Table 1. Usage of different individual knots in the experiment, with respect to the factors prey species, size and depth. Each entry lists the individuals (Table 2) in each particular treatment, giving the individual number as often as the bird was used. Density gives number of bivalves per tray

Species	Density	Prey depth	Shell length					
			6 mm	8 mm	10 mm	12 mm	14 mm	16 mm
<i>Cerastoderma</i>								
	7	0.25 cm	—	—	—	35	—	—
	20	0.25 cm	2345	—	1234	—	—	—
	30	0.25 cm	—	1234	—	—	—	—
	35	0.25 cm	—	—	245	—	—	—
	75	0.25 cm	12345	12345	2345	45	—	—
<i>Macoma</i>								
	< 16	1 cm	—	4	—	14	11122344	4
		2 cm	—	—	1234	1	3	—
		3 cm	—	—	4	1	—	—
	16–35	1 cm	—	14	1344	22444444	14	4
		2 cm	—	4	1222234444	112244	12	—
		3 cm	—	—	4	—	4	—
	36–55	1 cm	—	14	—	—	4	4
		2 cm	—	—	—	1135	4	—
		3 cm	—	4	44	44	244	—
	> 55	1 cm	—	4	4444	—	1	—
		2 cm	—	1	4	344	1	—
		3 cm	—	4	14	4	—	—

Table 2. Characteristics of the five knots used in feeding experiments. Body mass was measured regularly during the experiments and the averages (with SD in brackets) are based on about 50 weighings per bird

Identity	Age	Body mass (g)	Bill length (mm)	Touch area (mm ²)	Putative subspecies
1	2nd c.y.	122.5 (8.1)	34.9	21	<i>islandica</i>
2	2nd c.y.	106.5 (6.1)	33.7	22	<i>islandica</i>
3	2nd c.y.	105.5 (7.8)	31.4	23	<i>islandica</i>
4	> 2nd c.y.	111.9 (12.8)	36.7	25	<i>canutus</i>
5	> 2nd c.y.	118.7 (10.9)	35.6	23	<i>islandica</i>

c.y. = calendar year.

of the flock in part of the cage. Air temperature in the experimental room was kept constant at 18°C. Prior to each experiment, birds were starved for c. 16 h. In this way we ensured that the knots were always motivated to feed at similar and fairly constant levels, but it lead them to have rather low body masses throughout the study (Table 2). At masses between 100 and 120 g, knots contain little fat (e.g. Piersma & Poot 1993). Between experiments, they were fed with hard-shelled mussels (*Mytilus edulis* Linné, 1758) in order to maintain their muscular stomach (Piersma, Koolhaas & Dekinga 1993c). Seawater and freshwater were always freely available.

BENTHIC PREY ANIMALS

Macoma and *Cerastoderma* were collected on the intertidal flats in the western Wadden Sea, 2–6 weeks before the experiments. *Mytilus* was scraped from piers in the North Sea on Texel. Immediately after collection, the bivalves were sorted according to size, measuring the maximal longitudinal length in 2 mm

classes. The assorted bivalves were kept in seawater basins at temperatures between 5 and 12°C. All bivalves remained alive for at least 2 months.

EXPERIMENTAL PROCEDURES

During each experimental session one bird was chosen to feed separately from its flock mates which remained visible and nearby. The tray on which the birds fed measured 0.25 m² and was filled with sandy sediment collected in the Wadden Sea (median grain size = 224 µm). Between 0.5 and 1.5 h before the start of an experimental session the prey were randomly distributed over the tray. The molluscs were put in the sediment in their natural position. For the bivalves this was done by pushing the animal in the appropriate upright position into the sediment using a plastic rod with depth indicators (either 1, 2 or 3 cm measured between the upper edge of the shell and the surface of the sediment in *Macoma*, and always 0.25 cm in *Cerastoderma*, close to the natural range in their depth in the field according to Zwarts & Wanink 1989).

Densities offered varied between 8 and 100 *Macoma* per feeding tray and 7–75 *Cerastoderma* per feeding tray. These figures correspond to the natural variation in densities encountered in the western Wadden Sea where knots occur (Piersma *et al.* 1993b).

Before every experimental session the penetrability of the sediment was measured by a spring penetrometer. Five spots on the tray were penetrated. If necessary, penetrability values were adjusted to the standard average value by adding some water or sand to the trays before positioning the bivalves.

Each of the 124 experimental sessions lasted until the birds had taken six prey. The first prey was excluded from the analysis, since at the start of an experiment search time for the first was hard to measure accurately. A high-resolution video camera registered all experiments. The video-images were examined. Search times for each successively ingested prey were measured at normal recording speed. Handling times were measured by slowing down the video-tape to one-fifth of the recording speed.

We checked whether our method of pushing bivalve prey in the sediment with a rod, and then filling and covering the hole, provided cues to the feeding knots. Four birds were let foraging on a tray in which at one third of previously randomly assigned coordinates, prey were inserted in the sediment. At another third, holes were made and filled again without a prey being inserted. The remaining third of the coordinates was left untouched. We allowed the birds to forage for 5 min, and then examined the sediment for pecks and probes to see whether they aimed their probes randomly over the tray or whether they cued into filled holes, either containing a *Macoma* or not. We tested this by comparing the numbers of pecks and probes within a radius of 1.5 cm around the different 'hole' types at the assigned coordinates.

STATISTICAL ANALYSES

Several linear models, differing in the factors taken into account, were examined. Dependent variables were the average search time and the average handling time of the second to the sixth prey encounters. We assumed that during the short interval in which the birds encounter the first six prey items, searching was more or less systematic, so that the effect of prey depletion could be ignored. Normal probability plots showed that both variables were approximately normally distributed after log transformation. Logs to the base 10 were used. The *Macoma*- and *Cerastoderma*-sessions were analysed separately.

In accordance with Holling's deterministic model, the simplest stochastic models for the random variable search time, T_s , leads to:

$$E[T_s] = \frac{1}{a} \frac{1}{D} \quad \text{eqn 4}$$

or:

$$E[\log(T_s)] = -\log(a) - \log(D) \quad \text{eqn 5}$$

where $E[X]$ is the expectation of X , and a is constant and independent of shell length, depth and individual bird. To account for the latter series of effects we started with a generalization of the model which is equivalent to the following analysis of variance model (our Model 1):

$$\log(T_s) = b_0 + L_i + P_j + B_k + D_l + \varepsilon \quad \text{eqn 6}$$

where L_i is the effect of length class i , P_j is the effect of prey depth class j , B_k is the effect of individual bird k , D_l is the effect of density class l and ε is an independent and identically normally distributed error.

Next, more simple linear models were examined, for example:

$$\log(T_s) = b_0 + b_1 \log(L) + P_j + B_k + b_2 \log(D) + \varepsilon \quad \text{eqn 7}$$

where a linear relationship between $\log(T_s)$ on the one hand and $\log(L)$ and $\log(D)$ on the other hand is assumed (Model 2). Model 3 is even more restrictive in its assumptions. Applying the extra sum of squares principle, models were tested against each other using the F -test (Wetherill 1986). Finally, hypotheses concerning the parameters b_1 and b_2 were tested, i.e. $b_1 = 0$ and $b_2 = -1$ (Model 4). Both parameter values follow from considerations given above. A similarly structured analysis was performed for handling time, T_h .

All analyses were performed using SYSTAT (Wilkinson 1990).

Results

LOCALIZED PROBING DUE TO EXPERIMENTAL INSERTION OF PREY IN SEDIMENT?

Although the birds differed in the total number of probes and pecks administered to the sediment in the tray in 5 min (respectively 64, 154, 175 and 227), none of the individual birds appeared to cue into filled or unfilled holes (Table 3).

SEARCH AND HANDLING TIMES

All bivalve prey extracted from the sediment were ingested, so there was no problem of 'negative' handling times. For both prey species, *Cerastoderma* and *Macoma* (Fig. 1), no significant differences between the four search time models that were analysed could be discovered, i.e. no effects of shell length, prey depth and individual bird were found. Hence the simplest model (Model 4), in which search time is only a linear function of the inverse of density, should be preferred (Tables 4 and 5, and see Fig. 2). In Model 2 the parameter values for b_1 , the slope for $\log(L)$ were estimated at -0.14 for *Cerastoderma* and 0.56 for *Macoma*. Both values did not differ significantly from

Table 3. Outcome of the feeding experiments to ascertain whether our method of pushing 12 mm long *Macoma balthica* into the substrate (in this case to 2 cm) affected the feeding effort (pecks and probes) by the knots. For none of the birds the hypothesis of independence between 'hole' types (with *Macoma*, empty or control) and indication of feeding (unpecked vs. pecked) could be rejected (Monte Carlo estimate of exact likelihood ratio test, Cytel 1991)

Individual	Indication of feeding	Number of 'hole' types			P-value
		With <i>Macoma</i>	Empty 'hole'	Control location	
1	Unpecked	1	1	2	0.99
	Pecked	20	20	19	
2	Unpecked	6	6	6	0.99
	Pecked	15	15	15	
3	Unpecked	3	1	1	0.61
	Pecked	18	20	20	
4	Unpecked	6	10	9	0.53
	Pecked	15	11	12	

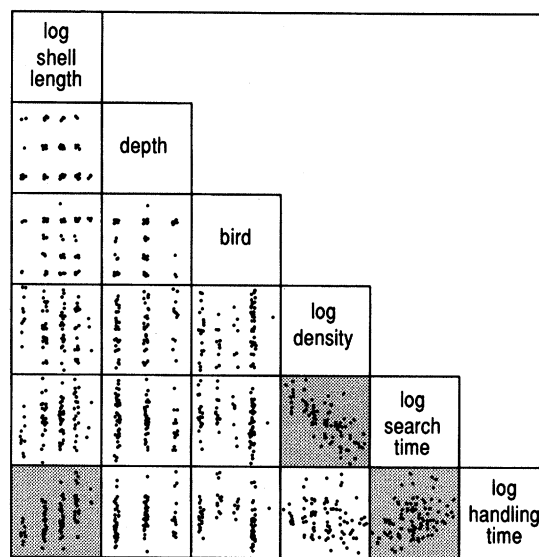


Fig. 1. Plots of all independent factors and variables (log shell length, individual bird and log density) and the two dependent variables (log search time and log handling time) against each other, for *Macoma balthica*.

Table 4. Analysis of variance table of four linear models of search time for *Cerastoderma edule*. Dependent variable is log (T_s). In Model 1, length, bird and density are category variables. In Model 2, bird is a category variable, and log (length) and log (density) are covariates. In Model 3, log (density) is the only covariate. In Model 4, the parameter for log (density) is set equal to -1 . SS is sum of squares, df is degrees of freedom, bold printed figures indicate a significant contribution ($P < 0.005$)

Model	1		2		3		4	
	df	SS	df	SS	df	SS	df	SS
Length	3	0.111	1	0.007	—	—	—	—
Bird	4	0.299	4	0.334	—	—	—	—
Density	4	2.389	1	2.303	1	2.445	0	2.402
Error	21	1.057	26	1.373	31	1.734	32	1.777
R^2		0.75		0.67		0.59		0.57

Table 5. Analysis of variance table of four linear models of search time for *Macoma balthica*. Dependent variable is log (T_s). In Model 1, length, prey depth and bird are category variables, and log (density) is a covariate. In Model 2, bird and prey depth are category variables, and log (length) and log (density) are covariates. In Model 3, log (density) is the only covariate. In Model 4, the parameter for log (density) is set equal to -1 . SS is sum of squares, df is degrees of freedom, bold printed figures indicate a significant contribution ($P < 0.05$)

Model	1		2		3		4	
	df	SS	df	SS	df	SS	df	SS
Length	4	0.341	1	0.168	—	—	—	—
Prey depth	2	0.002	2	0.005	—	—	—	—
Bird	4	0.291	4	0.316	—	—	—	—
Density	1	6.033	1	6.505	1	8.844	0	8.765
Error	79	6.456	82	6.629	89	7.179	90	7.259
R^2		0.60		0.59		0.55		0.55

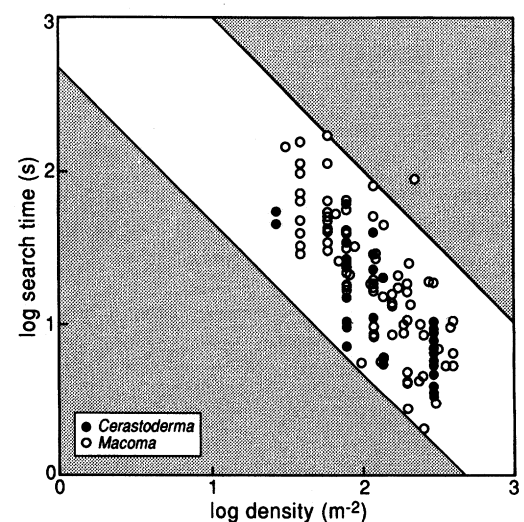


Fig. 2. Search time as function of prey density in knots feeding on *Cerastoderma edule* (closed dots) and *Macoma balthica* (open circles). Every symbol indicates the result of one experimental session (see Tables 4 and 5 for statistics). The open area with data points is bordered by slopes of -1 .

zero. In Model 3, in which shell length and bird were excluded, the parameter values for b_2 , the slope for $\log(D)$, were equal to -0.88 and -1.11 for *Cerastoderma* and *Macoma*, respectively. Both values did not differ significantly from -1 , leading to Model 4 (Fig. 2). The parameter a , the instantaneous area of discovery, was estimated from: $\log(T_h) + \log(D) = -\log(a) + \varepsilon$. Because all analyses were performed on log-scale, a simple back-transformation (the antilog of the estimate) will yield the geometric instead of the arithmetic mean. We therefore applied the bias correcting back-transformation (i.e. antilog (estimate $+ 2.303$ variance/2)), yielding $a = 6.4 \text{ cm}^2 \text{ s}^{-1}$ for *Cerastoderma* and $a = 5.2 \text{ cm}^2 \text{ s}^{-1}$ for *Macoma*.

Similarly, for handling time the simplest model (Model 4) in which handling time can be described by a linear function of shell length squared, yielded the best fit (Tables 6 and 7, and see Fig. 3). However, handling time also differed among individual birds, and (for *Macoma*) among depth classes. For Model 3

the parameter values for b_1 were equal to 2.11 and 1.87 for *Cerastoderma* and *Macoma*, respectively. These values did not statistically differ from 2 (handling time being related to shell surface area), leading to Model 4. Back-transformed parameter values for prey depth and bird effects are given in Table 8.

Discussion

INGESTING PREY WHOLE: DIFFERENCES BETWEEN KNOTS AND AN OYSTERCATCHER

Wanink & Zwarts (1985) concluded that oystercatchers did not obey the disc equation when feeding on buried bivalve prey (in their study: *Scrobicularia plana* [Da Costa, 1778]), since both the instantaneous area of discovery (a) and the handling time (T_h) decreased with increasing prey density instead of being constant. As we have seen, the assumptions are obeyed by knots who show no density effects on handling time (Tables 6 and 7). The negative correlation between prey density and a in oystercatchers was attributed by Wanink & Zwarts (1985) to an increased selectivity of the bird for particular individual prey at higher densities of buried bivalves. Heightened selectivity would also explain the decrease in handling time with increasing prey density, since oystercatchers are likely to select increasingly the bivalves from which the flesh can be most easily extracted (such as those with valves slightly agape allowing the easy insertion of the bill). Knots ingest their bivalve prey whole, and this additional criterion does not apply. The fact that oystercatchers extract flesh from the shell whereas knots ingest them whole, may therefore explain the differences in the extent to which these two probing wader species obey the two basic assumptions of the disc equation.

THE HOLLING DISC EQUATION AND TOUCH-VARIANTS

As pointed out by Getty & Pulliam (1993), a itself tells us nothing about the actual prey detection process since identical values of a could characterize very different feeding and detection modes. However, by comparing empirical values of a with predictions based on explicit detection models, such as the touch-model for probe-feeding birds, such inferences can be drawn.

For a probe-feeding bird, the instantaneous area of discovery, a ($\text{cm}^2 \text{ s}^{-1}$), is usually assumed to be the product of the effective touch area and the probing rate. The effective touch area, A_{eff} , is determined by the horizontal area occupied by the tip of a slightly opened probing bill, A_{bill} (this area might differ among individual birds). The part of the feeding area in a horizontal plane that is occupied by prey is the touch area of the hard-shelled prey, A_{shell} . If we combine this with A_{bill} , we obtain the effective touch area (A_{eff} ; see Hulscher 1982 and Zwarts *et al.* 1992). To simplify

Table 6. Analysis of variance table of four linear models of handling time for *Cerastoderma edule*. Dependent variable is $\log(T_h)$. In Model 1, length, bird and density are category variables. In Model 2, bird is a category variable, and $\log(\text{length})$ and $\log(\text{density})$ are covariates. In Model 3, bird is a category variable, and $\log(\text{length})$ is the only covariate. In Model 4, the parameter for $\log(\text{length})$ is set equal to 2. SS is sum of squares, df is degrees of freedom, bold printed figures indicate a significant contribution ($P < 0.05$)

Model	1	2	3	4
	df SS	df SS	df SS	df SS
Length	3 1.284	1 1.471	1 1.564	0 1.559
Bird	4 0.411	4 0.389	4 0.393	4 0.388
Density	4 0.107	1 0.003	— —	— —
Error	21 0.272	26 0.383	27 0.386	28 0.391
R^2	0.88	0.83	0.83	0.83

Table 7. Analysis of variance table of four linear models of handling time for *Macoma balthica*. Dependent variable is $\log(T_h)$. In Model 1, length, prey depth and bird are category variables, and $\log(\text{density})$ is a covariate. In Model 2, bird and prey depth are category variables, and $\log(\text{length})$ and $\log(\text{density})$ are covariates. In Model 3, bird and prey depth are category variables, and $\log(\text{length})$ is the only covariate. In Model 4, the parameter for $\log(\text{length})$ is set equal to 2. SS is sum of squares, df is degrees of freedom, bold printed figures indicate a significant contribution ($P < 0.05$)

Model	1	2	3	4
	df SS	df SS	df SS	df SS
Length	4 2.280	1 1.859	1 1.924	0 1.914
Prey depth	2 0.667	2 0.487	2 0.526	2 0.545
Bird	4 1.779	4 1.679	4 1.752	4 1.751
Density	1 0.003	1 0.000	— —	— —
Error	79 2.054	82 2.474	83 2.475	84 2.484
R^2	0.71	0.65	0.65	0.65

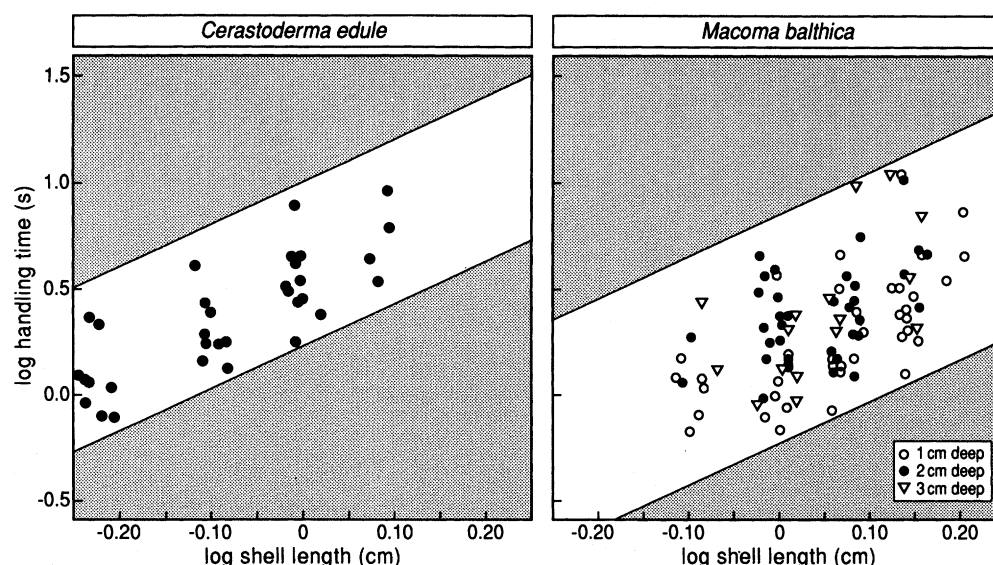


Fig. 3. Handling time as function of shell length in knots feeding on *Cerastoderma edule* and *Macoma balthica*. Every symbol indicates the result of one experimental session (see Tables 6 and 7 for statistics). The open area with data points is bordered by slopes of 2.

Table 8. Back-transformed parameter values for Model 4, in which the estimated handling time (s) is a constant ($s \text{ cm}^{-2}$) times prey depth effect (–) times individual bird effect (–) times squared shell length (cm^2)

Parameter	<i>Cerastoderma</i>	<i>Macoma</i>
Constant	3.44	2.23
Prey depth 1 cm	–	0.79
Prey depth 2 cm	–	0.96
Prey depth 3 cm	–	1.31
Bird 1	0.97	0.84
Bird 2	1.49	1.59
Bird 3	0.99	1.21
Bird 4	0.71	0.62
Bird 5	0.98	0.99

itself suggests that deeply buried bivalve prey are not found by touch alone. Nevertheless the touch-model gives a good fit to the observed intake rates of shallow buried *Cerastoderma* (Fig. 4), especially if we take into account that successive probes show overlap. For small-sized and deeply buried *Macoma*, however, the observed intake rates are usually greater than predicted from the touch-model (Fig. 5), even if an increase in the effective touch-area by a widening of the gape is accounted for. Along the Friesian fore-shore knots were feeding on particularly large (Zwarts & Blomert 1992: figs 6 and 13) and shallow living (Zwarts *et al.* 1992: fig. 9) *Macoma*. This made it impossible to distinguish between the touch and

the calculations the shape of the bill tip is taken as a rectangle, with a width (w ; is *c.* 0.7 cm, measured from imprints in soft sediment) and a thickness (t ; is *c.* 0.3 cm). The touch area of the shell can be represented as a circle, with a radius (r). We used Zwarts & Blomert's (1992: fig. 11) regression lines describing the relationships between measured A_{shell} and shell length to derive r for different shell length categories. Then the effective touch area, A_{eff} , can be calculated as $A_{\text{eff}} = wt + 2wr + 2tr + \pi r^2$ (Zwarts *et al.* 1992: fig. 1). This approach assumes that the effective touch areas of successive probes do not overlap. If knots detect buried bivalve prey by touch we would expect that: (i) a increases with shell length (Zwarts & Blomert 1992); and (ii) a decreases with prey depth, since the passage rate of the bill-tip is an inverse function of probing depth, with the probing rate at a depth of 3 cm being only 10% of that on the surface (unpublished data obtained during these experiments). Neither prediction was borne out, neither prey size nor prey depth affecting the instantaneous area of discovery. This in

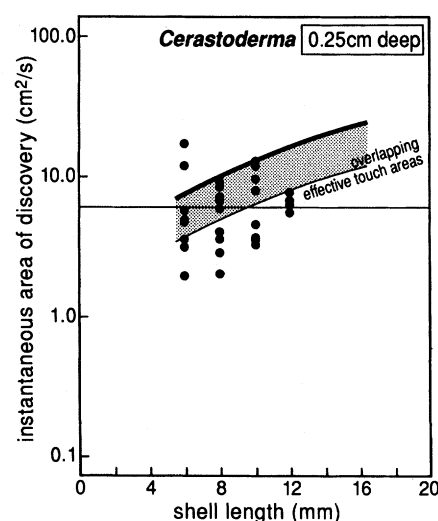


Fig. 4. The observed instantaneous area of discovery, a (i.e. $1/(T_s D)$), of knots feeding on *Cerastoderma*, in comparison with the estimated average from Model 4 (horizontal line, see Table 4) and the prediction of Zwarts & Blomert (1992) (thick curve, see legend Table 5) corrected for 50% overlap between surface pecks (lower edge of shaded area).

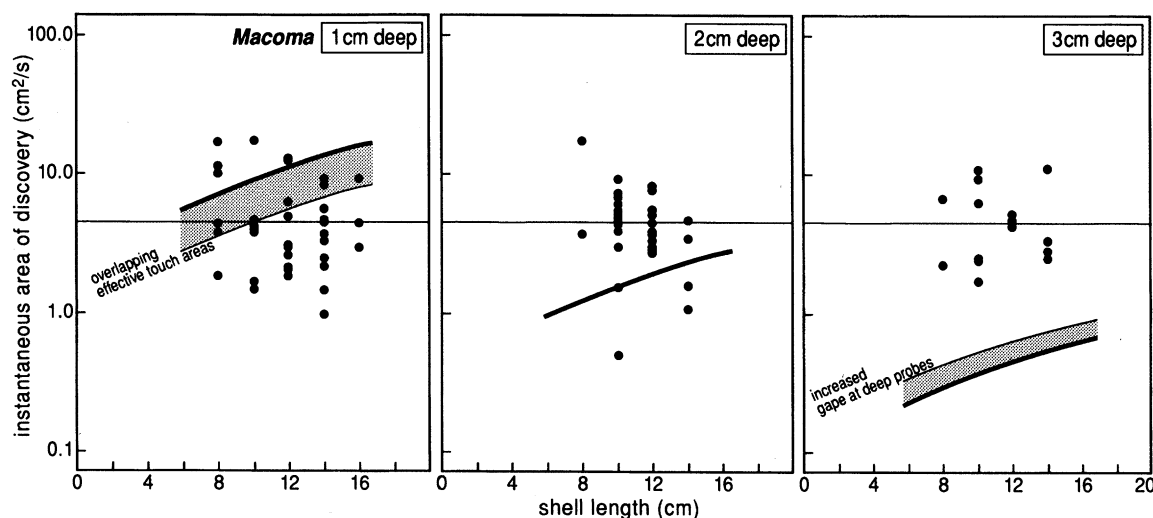


Fig. 5. Observed instantaneous area of discovery, a (i.e. $1/(T_s D)$), of knots feeding on *Macoma*, at different depths in comparison with the estimated average from Model 4 (horizontal line, see Table 5) and the predictions of Zwarts & Blomert (1992) (thick curves, incorporating adjustments for effective probe rates other than $1.6 \text{ probes s}^{-1}$ at depths shallower and deeper than 2 cm: $9.6 \text{ probes s}^{-1}$ at depths than 1 cm or smaller and $0.4 \text{ probes s}^{-1}$ at 3 cm depth; personal observations), corrected for 50% overlap between surface pecks (i.e. effective probe rate of $4.8 \text{ probes s}^{-1}$, indicated by lower edge of shaded area for 1 cm deep *Macoma*) or the opening of the bill during deep probes (a bill-tip width of 1.2 cm rather than 0.7 cm, indicated by upper edge of shaded area for 3 cm deep *Macoma*).

'remote sense' variants, and it explains the agreement found by Zwarts *et al.* (1992) between the measured intake rate of knots and the prediction based on the touch-model (Zwarts *et al.* 1992: fig. 11).

REMOTELY SENSING LIVING BIVALVES?

The fact that observed intake rates and instantaneous areas of discovery, particularly of small and deep living bivalves, are higher than predicted by the touch-model, suggests that knots are using some sort of 'remote sense' (*sensu* Gerritsen & Meijboom 1986) to locate buried bivalve prey. It confirms the distinction, suggested by these authors, between a 'tactile direct' feeding style used by oystercatchers, and a 'tactile remote' feeding style used by sanderlings and other sandpipers with a diet of polychaetes crawling sub-surface in the sediment. What would be the kind of remote sense employed by knots?

It is difficult or impossible to get directional information from tasting or smelling the prey in the sediment where water or air flow would be limited (Dusenbery 1992). Although knots have been shown to possess taste, they appear to ignore the taste information in microhabitat selection (Gerritsen *et al.* 1983), in contrast to three other sandpiper species (van Heezik, Gerritsen & Swennen 1983). Excluding further the possibility of detection of very weak electric fields around buried prey (Dusenbery 1992), knots might therefore use the sanderling-system of remotely sensing moving prey on the basis of high frequency (300–1000 Hz) vibrations (Gerritsen & Meijboom 1986; Gerritsen 1988b), picked up by the numerous Herbst corpuscles found in the bill tip of sandpipers

(Bolze 1968; Hoerschelmann 1970, 1972; Pettigrew & Frost 1985; summary in Gerritsen 1988b). Alternatively, if buried prey would not provide any vibrational information themselves, they could somehow learn from self-induced pressure signals. In the case of rather stationary buried bivalves like *Macoma*, which themselves show a whole range of short- and long-term predation-avoiding behaviours (Kamer-mans & Huitema 1994; personal observations), it seems unlikely that they would reveal their presence by moving through the sediment when flocks of predatory waders wander over, or when terrified after repeated handling as during the experimental sessions reported here.

We could think of two pressure mechanisms which could be used by knots to discover deeply buried bivalves: (i) that knots, by the rapid movements of their bill in the substrate at a frequency of about 10 Hz, would generate a wave of which they would receive back the reflections; and (ii) that they would register the build-up of pressure in the direction of a solid object as the bill moves into the sediment. The first mechanism would require a sensor capable of picking up low frequency pressure waves, such as the Grandry corpuscles, which are able to detect frequencies up to 150 Hz, mentioned by Gerritsen (1988b). However, the resulting wavelength of 100 m (Dusenbery 1992: table 9-3) would no doubt be prohibitive. The second mechanism requires as yet undescribed specialized mechanoreceptors in the bill tip. As pointed out by Dusenbery (1992: p. 258), touch stimuli and sensors, let alone remote-sense mechanisms, are both very situation specific and hard to measure and manipulate.

Whatever the exact prey detection mechanism, the increased scope for exploitation of mollusc food stocks below the previously accepted threshold value deserves further quantification. We have analysed the distribution of knots and *Macoma* and *Cerastoderma* on the intertidal flats around the small island of Griend in the western Wadden Sea in August–September 1993 (see Piersma *et al.* 1993b for an account of the distribution and abundance and diet of knots in this area in previous years). The analyses of locally collected faeces (Dekinga & Piersma 1993) and visual observations, showed that *Cerastoderma* and *Macoma* contributed over 95% of the diet, with *Cerastoderma* taking the largest share. On the basis of the measured size and depth distributions of *Macoma* and *Cerastoderma*, and assuming no interference (Sutherland 1983) during experiments (obvious, with one bird feeding at a time) and in the field (Goss-Custard 1970, personal observations), it is possible to reconstruct separate functional response curves for both prey species based on the two models (our empirical model and the direct touch-model of Zwarts *et al.* 1992). From the observations of M. Poot & T. Piersma (unpublished) on daily energy expenditure of foraging knots and the weather-related maintenance cost estimates by Wiersma & Piersma (1994), we infer that knots in August–October would require a minimum intake rate of about 0.3 mg ash-free dry mass s^{-1} feeding time, if they feed continuously for 10 h per day. We furthermore assume that individual knots specialize to feed on one bivalve species at a time, yielding conservative estimates of the extent of suitable area.

For the deep-living *Macoma* the two models generate rather different functional response curves (Fig. 6A). The touch-model gives lower intake rates, and a higher threshold of acceptable harvestable biomass (Fig. 6A), than the 'remote sense' model. In the shallow living *Cerastoderma* the difference between the models is small, and so are the predictions for biomass thresholds (Fig. 6B). An analysis of the spatial distribution of the two bivalves around Griend shows that, on the basis of the empirical functional response curve for *Macoma*, knots could occur over a much wider area of intertidal flat than on the basis of the direct touch-model (Fig. 6C: 59 squares of 250×250 m instead of 6). The predictions on the basis of *Cerastoderma* are similar (Fig. 6D). It is rewarding to find that the concurrent distribution of feeding knots (Fig. 6E), shows a strong overlap with areas where the threshold biomass is reached (Fig. 6F), 43 (86%) of the 50 flock occurrences being at suitable sites. Of these 43 sites, 42% were suitable due to the harvestable biomass of *Macoma* exceeding threshold levels, 37% were due to *Cerastoderma* being sufficiently abundant, and at 21% of the sites both bivalves showed har-

vestable biomasses above threshold values. Even if flocks could be 100% accurately localized, we would not expect a perfect correspondence between the biomass and knot-distribution maps since knots are bound to also sample unrewarding parts of the flats since prey abundance probably cannot be visually judged from a distance.

Thus, we can account for the absence of knots in intertidal areas to the far southwest, northwest and north of the island of Griend and their occurrence in areas with small harvestable biomass values of *Macoma*. This explains much of the discrepancy between the findings of Zwarts *et al.* (1992) and Piersma *et al.* (1993b) for the harvestable biomass thresholds for *Macoma* in relation to the occurrence of knots in different intertidal areas, as discussed by the latter authors.

GENERALIZATION

Many formal models for the distribution of predators over different patches of habitat subsume a type-2 functional response of intake rate on prey abundance (Sutherland 1983; Kacelnik, Krebs & Bernstein 1992). Tests of these models concentrate on an evaluation of the predictions, notably on the question of whether intake rates, the combined result of functional response and interference, are equal across habitat patches. The form of, and the assumptions underlying, these separate components usually are not examined (Parker & Sutherland 1986; Kacelnik *et al.* 1992). Here we have successfully analysed and reconstructed the functional response of knots feeding on bivalves (even though the precise prey detection mechanism is still unknown), but we have not used it to the full by examining all possible formal models for the distribution of knots over different parts of their intertidal habitat. Still, the good quantitative agreement between the spatial distribution of feeding flocks and the minimally suitable prey stocks as predicted from the empirical disc equation, suggests that relatively simple systems like knots feeding on bivalves are amenable to such comprehensive analyses. In general, detailed analyses of functional responses provide two-edged swords: (i) contrasts with explicit detection models may suggest possible prey detection mechanisms; and (ii) they generate the parameter-values necessary as input in explicit models of predator distributions.

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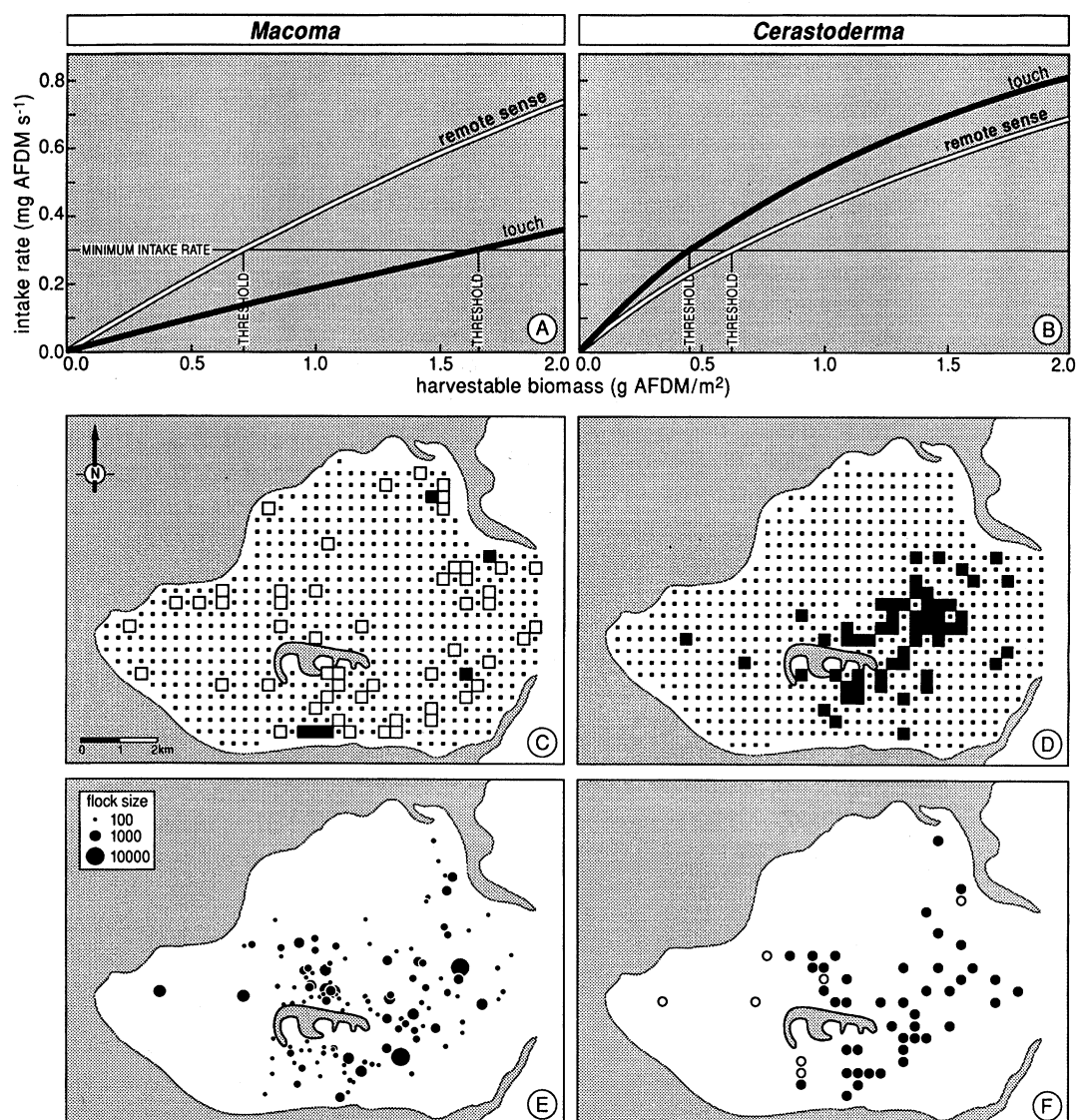


Fig. 6. Implications of two functional response models with different sets of assumptions on the prediction as what counts as suitable intertidal flat for the situation around the island of Griend in the western Wadden Sea in August–September 1993. The two models are: (i) the touch-model (50% overlap between probes down to 1 cm, but no increased gape; see Fig. 5) of Zwarts *et al.* (1992); and (ii) the 'remote sense' model using values for instantaneous area of discovery (*a*) on the basis of this study. Both models use handling times as determined in this study. (A) and (B) display the resulting functional response curves for *Macoma* and *Cerastoderma*, respectively, along with the biomass thresholds given that knots require a minimal intake of 0.3 mg ash-free dry mass s⁻¹. Maps (C) and (D) show the island (grey area in middle), the extent of intertidal flat (white) and the 250 × 250 m squares which contain biomass densities higher than the threshold values on the basis of the two models as derived in (A) and (B). In (C) open squares indicate that the area contains enough *Macoma* according to the remote sense model, and filled squares that it is even suitable according to the touch model. Since the predictions of harvestable biomass thresholds for *Cerastoderma* by the two models are quite similar, only filled squares are shown in (D) to indicate suitable areas. (E) shows the distribution of foraging knot-flocks of different sizes encountered during all stages of low tide in August and September 1993, and (F) the distribution of flocks of at least 500 knots: filled dots indicate that they border or overlap with suitable squares, open circles that they do not.

NIOZ tolerated the occasional salt-sandy mess, and a lot of Potvis comrades assisted in caring for the knots, whether collecting mussels in the surf or checking birds during weekends. The 1993 field season was made a success through a diligent voluntary workforce comprised of Aarno Karels, Ferdinand Borsje, Bernd Riedstra, Jan Drent, Elisabeth Dillmann and Erwin Adema, with transport and provisions provided by Kees de Boer, Jan van Dijk, Dirk Kuiper, the

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